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COOPERATIVE DEFENSE AND INTRASEXUAL AGGRESSION IN SCOPS OWLS (*OTUS SCOPS*): RESPONSES TO PLAYBACK OF MALE AND FEMALE CALLS

PAOLO GALEOTTI, ROBERTO SACCHI AND ELENA PERANI
Laboratorio di Eco-Etologia dei Vertebrati, Dipartimento di Biologia Animale, Università di Pavia, Italy

ABSTRACT.—We tested 11 male Scops Owls (*Otus scops*) and their mates with the playback of conspecific male and female calls to determine whether their response to intruders differed according to the sex of the intruder. Eight measures of response intensity were recorded for each owl. Territorial defense appeared to be strictly cooperative with both members of a pair reacting to intruders of either sex. Males responded more strongly to male playbacks for five measures of response intensity indicating that males are more aggressive toward intruding males. Females also showed a tendency to respond stronger to female playbacks, but, overall, both sexes showed little reaction to female calls. This may provide a mechanism for polygyny in this species.

KEY WORDS: Otus scops, *Scops Owl, cooperative nest defense, intrasexual aggression, territory defense.*

Defensa cooperativa y agresión intrasexual en *Otus scops*: reacción a repetición de llamadas en machos y hembras

RESUMEN.—Nosotros examinamos 11 machos de *Otus scops* y sus hembras con la repetición del ululato de macho y hembras conspecificos para determinar si su reacción para intrusos era diferente segun el sexo del intruso. Ocho medidas de contestacion intensidad fueron grabadas para cada búho. Defensas territorial aparecieron ser estrictamente cooperativo en este especie con los dos miembros reaccionando a intruso de cada sexo. Macho reaccionaron mas agresivos a repeticiones de machos que sus hembras pero no habia diferencia a la repetición de hembras, con los dos sexos demonstrando poco reacción al ululato de la hembra. Esta puede demonstrar un mecanismo de polygyny en este especie.

[Traducción de Raúl De La Garza, Jr.]

Studies of territorial birds have shown that males and females react to intruders of their own sex but do not cooperate in territorial defense when intruders are of the opposite sex (Arcese et al. 1988, Arcese 1989, Gerrard et al. 1992). Such intrasexual aggression is not surprising because the loss of breeding territory is very likely to decrease a bird's fitness. On the other hand, if intruders are of the opposite sex, territory holders may not be directly threatened, and might even benefit from polygamy or mate switching if their previous partner is an inefficient forager or a bad parent.

In many monogamous bird species, both members of a pair cooperate in territorial defense against single intruders of either sex (Hirons 1985, Ritchison 1986, Ens et al. 1993). Two hypotheses have been proposed to explain such cooperative territory defense. If pair-bond maintenance affects breeding success in some way (Perrins and McCleery 1985, Bradley et al. 1990), then a male attacking a female intruder and a female attacking a male intruder might be the expression of their reciprocal interest in retaining their mate on the territory. On the other hand, partners may simply be involved in mutualistic defense, where males and females help one another defend against intruders (Ens et al. 1993). Both members would benefit from participation in this type of defense without assuming they have an interest in retaining their current partner on the territory.

We tested some of these hypotheses using the Scops Owl (*Otus scops*) as a model. It is a migratory, nocturnal raptor which defends multipurpose territories during breeding season (Cramp 1985). It is essentially monogamous but polygamy can occur (Koenig 1973), and some degree of sociality (loose colonies) has been observed (Galeotti and Gariboldi 1994). Therefore, a study of aggressive behavior in male and female Scops

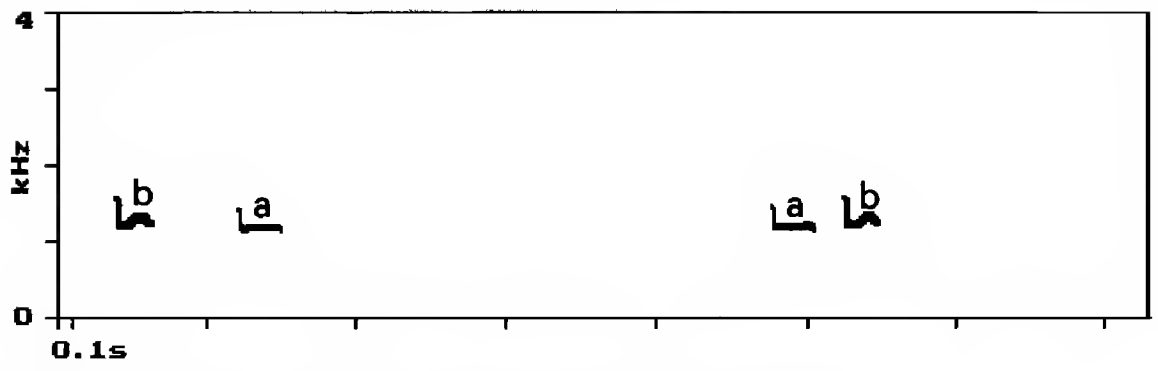

Figure 1. Sonograms of the calls of male (a) and female (b) Scops Owls.

Owls may help us better understand mechanisms producing different mating and dispersal strategies in owls.

We expected males to react more strongly to males and females to females. If pair-bond maintenance affected patterns of territorial defense, we expected members of long-established pairs to respond with the same intensity to intruders of any sex compared to members of more recently-established pairs. Alternatively, if partners were involved in a reciprocal altruistic system, they should cooperate independently of pair-bond length.

METHODS

The study was carried out in the Oltrepò Pavese, a hilly area (450 km^2) south of Pavia city in northern Italy. Altitude ranges between 100–600 m and the habitat consists of vineyards, orchards and cereal croplands. Wooded areas are scarce and mainly concentrated along rivers. Villages are scattered throughout the area.

The Scops Owl population in the study area was intensively studied from 1992–95. During this period, the population declined from a high of 37 Scops Owl pairs in 1992 to 20 pairs in 1995. Most territories (75%) were defended by a pair each year and it was rare to find territories where only single owls were found.

Scops Owls arrive in the study area in late March and stay until late September. Territorial behavior (vocal display) starts after arrival and peaks in April–May; thereafter, it decreases and most birds appear to defend only a small area around their nest sites. Egg laying and incubation starts in late May–early June, and parental care continues throughout July and August.

The vocal repertoire of the Scops Owl is dominated by its territorial call, a musical, clear and bell-like hoot, "kyü," that sounds disyllabic and is repeated monotonously for hours during warm, calm nights. Each male calls in its own rhythm and its own pitch (van der Weyden 1975, Galeotti, unpubl. data) and is therefore individually recognizable. Females also call, especially in synchronized antiphonal duets (Fig. 1) with their mates (Koenig 1973, Galeotti unpubl. data). Vocal exchange between rival males is clearly distinguishable from male-female duetting by the lack of synchrony in the former calls. The calls of male and female Scops Owls are distinguishable in the field and through the use of sonograms because female calls are more disyllabic, have a lower amplitude, and a higher pitch compared to those of males (Koenig 1973, Voous 1988): 1400 Hz, SD = 0.08, range 1320–1700, N = 12 vs. 1250 Hz, SD = 0.09, range 1130–1530, N = 21 (Galeotti, unpubl. data). Alarm, anger, and copulation solicitation calls are also known (Koenig 1973) but they are simple vocalizations (shrill or hiss) that are given by both males and females in typical situations outside territorial contests.

We compared responses of male and female Scops Owls to the playback of conspecific hoots of their own and of the opposite sex. Playbacks were conducted on calm dry nights from 2000–2400 H between 5–28 May 1994. We tested 11 pairs, whose territories had previously been mapped in April. For the tests, we used tapes of males and females that had been recorded in the same study area in the previous years (SONY IC TCM-R3 tape recorder, Sennheiser MD21N dynamic microphone, aluminium parabola diameter 60 cm), but that were unfamiliar to the owls tested because adjacent territories were >10 km apart. Sexes of recorded owls were determined from behavior, when possible (e.g., only females incubate), and on the basis of vocalizations (type and pitch). The use of unfamiliar hoots and the highly scattered distribution of pairs over the study area prevented us from using a larger sample of owls.

For all tested pairs, we used unique male and female stimuli (e.g., 11 different male playbacks and 11 different female playbacks) to avoid pseudo-replication (Kroodsma 1989). Responses of males and females of the same pair were recorded in the same test so that zero to four responses could be expected from each trial (up to two from the male and up to two from the female of the pair being tested).

As we were able to individually recognize responding males by spectrographically analyzing calls (Galeotti and Pavan 1991), we sorted them into two categories (first-settled owls and old-settled owls with 2–3 yr of continuous occupancy) on the basis of years territories had been occupied as determined by repeated recordings within the same territory. We recorded the tested females only in 1994 so we were unable to determine their turnover and the length of the pair bond in each territory. However, we assumed that first-settled males were newly mated compared to old-settled males which were mated for 2–3 yr.

We made playback tapes by selecting one call per owl and repeating it at 3-sec intervals for a total of 3 min (e.g., 20 calls/min, which corresponded closely to the natural rate of hoot delivery in our population). Playback

sessions were recorded on a cassette tape at a constant signal amplitude.

A playback test consisted of four consecutive sessions arranged in the following sequence (Galeotti and Pavan 1993): Playback 1 (PL1), 3 min; Control Period 1 (CL1), 17 min; Playback 2 (PL2), 3 min; Control Period 2 (CL2), 17 min. If PL1 was a male, PL2 would be a female and vice versa. The order of playback presentation was chosen at random.

Male and female calls were broadcast from an AIWA HS-JS 215 with an amplified loudspeaker (5 watt) placed in core areas of territories. The amplitude of playback (50 dBspl/m) was matched to the amplitude of natural singers (45–50 dBspl/m). To increase the validity of the experimental stimulus, we coupled playback with the presentation of a stuffed Scops Owl mounted on the speaker. Playback was not switched off when an owl responded, but ceased automatically after 3 min of stimulation.

All vocal responses were recorded for further analyses, and the following measures of response intensity were collected directly in the field by two observers, one of which was a "blind" observer who did not know anything about the experiment and simply recorded the behaviors of the owls. Both observers were hidden 10 m away from the playback recorder: (1) latency or the time in sec from the start of playback to the first response from the tested pair of owls, (2) distance in m of focal owls from the speaker at the time of first response to speaker, (3) nearest distance in m that owls approached to the speaker, (4) number of flights around the speaker, 5) number of "dive-bombing" flights or attacks above the stuffed owl. These behaviors were observed using light amplified binoculars (WILDT). From recordings, we also measured: (6) the number of calls, (7) the number of bouts, and (8) duration of each owl's response in sec.

We compared intensity of male and female responses to the paired and unpaired stimuli using a Wilcoxon matched-pairs signed-rank test. For these analyses we considered only responses of paired owls and discarded responses by single owls. We also compared responses of first- and old-settled males to the paired stimuli using a Wilcoxon test, while a Mann-Whitney U-test was used to compare responses of first- and old-settled males to the same stimulus. One-tailed tests were used only when the alternative to the null hypothesis was expected *a priori* to be in a specific direction.

RESULTS

From our 11 paired tests, we obtained a total of 34 responses. Males responded 19 times and females responded 15 times. One pair did not respond to the playbacks although both owls were observed to be on the territory at various times. We found no difference in any measure of agonistic response between the first and second tests at each nest indicating that the response to the second treatment was not conditioned by the preceding treatment.

Male and female responses did not differ by the sex of the playback owl. Males responded 10 times to male playbacks and 9 times to female playbacks. Females responded 8 times to male playbacks and 7 times to female playbacks (Fisher's exact test, $P = 1.0$). Females never responded alone regardless of the sex of the owl being played. Of male responses to playbacks of male calls, only two males responded alone while the other eight responded with their mates. Of male responses to female playbacks, again only two males responded alone indicating that Scops Owls are significantly more likely to respond to intruders with their mate than alone ($\chi^2 = 24.03$, df = 1, $P < 0.0001$).

Overall, the seven pairs of owls that responded to both male and female playbacks did not show stronger responses to intruders of their own sex (Table 1). Nevertheless, males tended to direct more attacks towards males than to females ($Z = 1.83$, $P = 0.034$, Wilcoxon one-tailed test) and females came closer to the speaker when responding to females ($Z = 2.02$, $P = 0.021$, same test). In addition, comparing male and female responses to the same stimulus, we found that males responded more quickly to male playbacks ($Z = 2.37$, $P = 0.009$, Wilcoxon one-tailed test), made more flights and attacks ($Z = 2.37$, $P = 0.009$), and called more ($Z = 1.86$, $P = 0.031$) than did females. Males also made more flights and attacks than did females when they responded to female playbacks but no further significant differences were detected between the sexes when they responded to female calls (all P-values > 0.06).

No significant differences in any measure of response intensity was found in either old- ($N = 5$) or first-settled ($N = 4$) males responding to both male and female playbacks (all P-values > 0.1, Wilcoxon two-tailed test). However, first-settled males generally gave more aggressive responses to male intruders than did old-settled males, although the difference was significant only for attack number ($Z_{6,4} = 1.93$, $P = 0.05$, Mann-Whitney U-Test). First- and old-settled males did not differ for any measure of response intensity to female playback (all P-values > 0.2, same test).

DISCUSSION

Despite its small sample size which made acceptance of the null hypothesis more likely, our study raises some interesting points concerning the defense of territories by Scops Owls against conspecific intruders. Our data indicate, for instance, that territorial defense is strictly cooperative in the Scops Owl with both members of a pair reacting

Table 1. Medians and interquartile range for each component of agonistic response by male ($N = 7$) and female ($N = 7$) Scops Owls to paired playbacks of male and female conspecific calls. Only pairs responding to both stimuli are included. *P*-values determined using a Wilcoxon one-tailed test; columns show response values to paired stimuli, rows show response values to the same stimulus by males and females.

VARIABLE	PLAYBACK	MALE	FEMALE	*P*
Latency (sec)	M	25 (44)	119 (102)	0.009
	F	54 (100)	149 (120)	0.17
	P	0.09	0.4	
First response (m)	M	80 (120)	80 (120)	0.33
	F	80 (87)	30 (63)	0.14
	P	0.07	0.02	
Nearest response (m)	M	10 (5)	10 (75)	0.09
	F	5 (5)	7 (5)	0.09
	P	0.5	0.054	
Flights (*N*)	M	3 (3)	1 (2)	0.017
	F	4 (3)	2 (3)	0.03
	P	0.15	0.18	
Attacks (*N*)	M	1 (6)	0 (0)	0.03
	F	0 (1)	0 (0)	0.09
	P	0.03	0.16	
Calls (*N*)	M	194 (145)	109 (118)	0.03
	F	167 (53)	152 (51)	0.2
	P	0.25	0.4	
Bouts (*N*)	M	11 (18)	11 (16)	0.34
	F	16 (7)	16 (6)	0.43
	P	0.33	0.29	
Duration (sec)	M	1045 (166)	858 (635)	0.06
	F	1038 (560)	1025 (465)	0.31
	P	0.25	0.23	

to intruders of either sex. Such cooperative defense behavior does not occur in Tawny Owls (*Strix aluco*). Like Scops Owls, male Tawny Owls defend against intruders of either sex but females are not defensive toward males when they intrude into their territories (B. Appleby and D. McDonald pers. comm.). This suggests that, unlike female Scops Owls that defend territories against intruding males, female Tawny Owls may be more prone to mate switching if intruding males successfully displace resident males.

We also found that responses by pairs of Scops Owls were more common than those of single birds. Partners often overlapped bouts of hoots in an antiphonal vocal duet. This finding was consistent with the theory that a joint response to intruders is more effective in maintaining territories (Ens et al. 1993). They may even prevent escalated contests reducing the risk of further attack and injury because a single intruder facing two defenders would likely give up more quickly.

The intensity of responses of territory holders did vary by sex with males responding fastest and attacking more often male than female intruders. Overall, females were noticeably less aggressive toward intruding males than were their mates and they never attacked intruding females while their mates sometimes did so. As female-female aggression may be of importance for the maintenance of monogamous pair bonds (Davies 1989, Veiga 1992), tolerance of intruding females by territorial female Scops Owls suggests that males might easily acquire a second mate at the beginning of the breeding season in order to maximize reproductive success. This may explain why male Scops Owls have a tendency to be polygynous if habitat quality and food availability are high (Koenig 1973).

If pair-bond length is an important determinant in the intensity of aggression, first-settled males should have reacted more differently to our playbacks than old-settled males. In fact, neither first- nor old-settled males differed significantly in the intensity of their responses to either male or female playbacks. Nevertheless, first-settled males

tended to respond more strongly to male than female intruders and they were more aggressive towards intruders of either sex than old-settled males. Further observations are necessary to determine whether the prevalence of polygamy increases in Scops Owls as territories are become occupied for long periods.

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